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EXTENSIVE MIGRATION IN BIRDS AS A CHECK UPON THE PRODUCTION OF GEOGRAPHICAL VARIETIES.

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Two problems have of late years received much attention from ornithologists, and deservedly, namely, the faunal distribution of species, and their ranges of migration. But to my knowledge, no one has raised the question of the possible existence of a relation between the extent of the periodic migration and the amount of geographical variation evinced by a species. The object of this paper then is to show that such a relation does exist, that extensive migration tends to act as a check upon the production of geographical varieties, or races so-called.

In the first place, on comparing the amount of faunal variation with the extent of the periodical migrations in a given species, it will be found to be usually, if not always, the case, that those species which undertake migrations of more than the average extent—migrating through 30° or more of latitude, have no tendency to give rise to geographical varieties. In order to see how far this law extends, and whether exceptions to it may be found, I have compared all the species of North American birds with regard to this relation existing between variation and range of migration, using Ridgway's excellent "Manual of N. A. Birds" as my authority for the amount of variation and extent of migration in these species. For our present purposes the North American species may be divided into three groups, based on the extent of their migrations: (1) species with exceedingly protracted migrations, but irregular as to the localities traversed; (2) species with more or less regular migrations, of 30° lat. or more in extent; and (3) species which undertake migrations less in extent than 30° lat., or species which do not migrate at all. We may now consider each of these groups in turn, with regard to the question at issue.

I. *Species with protracted but irregular migrations.*

<i>Diomedeidæ.</i>	<i>Phaethontidæ</i> (?)
<i>Procellariidæ.</i>	<i>Fregatidæ</i> (?)

II. *Species with a migration range of 30° lat. or more.*

<i>Podicipidæ.</i>	{ <i>Tyrannus</i> (2 species).
<i>Urinatoridæ</i> (all ?)	{ <i>Myiarchus crinitus.</i>
<i>Stercorariidæ.</i>	{ <i>Sayornis</i> (2 species).
<i>Laridæ</i> (most).	{ <i>Contopus</i> (3 species).
<i>Sulidæ</i> (most ?).	{ <i>Empidonax</i> (5 species).
<i>Anatidæ.</i>	{ <i>Dolichonyx oryzivorus.</i>
<i>Gruidæ.</i>	{ <i>Icterus galbula.</i>
{ <i>Rallus virginianus.</i>	{ <i>Calcarius.</i>
<i>Porzana.</i>	{ <i>Zonotrichia</i> (2 species).
<i>Fulica americana.</i>	{ <i>Spizella</i> (2 species).
<i>Phalaropodidæ.</i>	{ <i>Melospiza</i> (2 species).
<i>Recurvirostridæ.</i>	{ <i>Habia ludoviciana.</i>
<i>Scolopacidæ</i> (most).	{ <i>Passerina cyanea.</i>
<i>Charadriidæ</i> (most).	{ <i>Spiza americana.</i>
<i>Aphrizidæ.</i>	{ <i>Piranga</i> (3 species).
<i>Columbidæ</i> (most).	{ <i>Hirundinidæ.</i>
<i>Cathartidæ</i> (?).	{ <i>Vireo</i> (4 species).
{ <i>Circus hudsonius.</i>	{ <i>Mniotiltidæ</i> (most).
<i>Accipiter velox.</i>	{ <i>Motacillidæ</i> (most).
<i>Falco</i> (2 species).	{ <i>Galeoscoptes.</i>
<i>Ceryle alcyon.</i>	{ <i>Regulus</i> (2 species).
<i>Sphyrapicus varius.</i>	{ <i>Turdus</i> (3 species).
<i>Micropodidæ.</i>	
<i>Trochilus colubris.</i>	

Now the species enumerated in Lists I and II migrate periodically through an area of 30° lat., or more, that is, a migration range of considerable extent, and, with a few exceptions to be considered later, all are sharply defined species, and even though the breeding areas of most are very broad, none of them have a tendency to split into geographical varieties. Accordingly there must be some relation existing between

the range of migration and the tendency to produce geographical races, for otherwise this coincidence could not be explained. So having found that those species undertaking long migrations do not, as a rule, tend to give rise to local varieties, we must conclude that the process of taking extensive migrations is a check upon the tendency to produce geographical varieties. But in order to round off further deductions, we must first determine whether species which do not migrate extensively have a greater tendency to geographical variation than those just considered; and this assumption will be strengthened by a comparison of the species in the following List III with those in Lists I and II.

III. *Species with a short or no migration range.*

<i>Alcidæ.</i>	<i>Picidæ</i> (most).
<i>Rhynchops.</i>	<i>Caprimulgidæ</i> (most).
<i>Anhinga.</i>	<i>Trochilidæ</i> (most).
<i>Phalacrocoracidæ</i> (most).	<i>Cotingidæ.</i>
<i>Pelecanidæ.</i>	<i>Tyrannidæ</i> (most).
<i>Phœnicopterus.</i>	<i>Alaudidæ.</i>
<i>Plataleidæ.</i>	<i>Corvidæ.</i>
<i>Ibididæ.</i>	<i>Icteridæ</i> (most).
<i>Ciconiidæ.</i>	<i>Fringillidæ</i> (most).
<i>Ardeidæ</i> (most).	{ <i>Euphonia.</i>
<i>Aramidæ.</i>	{ <i>Piranga</i> (most).
<i>Rallidæ</i> (most).	<i>Ampelidæ.</i>
<i>Hæmatopodidæ.</i>	<i>Laniidæ.</i>
<i>Tetraonidæ.</i>	<i>Vireonidæ</i> (most).
<i>Phasianidæ.</i>	<i>Cœrebidæ.</i>
<i>Cracidæ.</i>	<i>Mniotiltidæ</i> (a few).
<i>Falconidæ</i> (most)	<i>Cinclidæ.</i>
<i>Strix pratincola.</i>	<i>Troglodytidæ</i> (most).
<i>Bubonidæ.</i>	<i>Certhiidæ.</i>
<i>Psittacidæ.</i>	<i>Paridæ.</i>
<i>Cuculidæ.</i>	<i>Polioptila.</i>
<i>Trogonidæ.</i>	<i>Turdidæ</i> (most).
<i>Momotidæ.</i>	
<i>Alcedinidæ</i> (most).	

It is at once apparent that almost all the species of North American birds which are divisible into geographical varieties are classed in this third list, that is, that those species evincing the greatest tendency to geographical variation, are also those which undertake migrations of the least extent. Thus, for instance, *Melospiza fasciata* is usually resident in most localities throughout the whole year, and has become differentiated into a number of geographical races, while *Melospiza georgiana* is migratory, and though it breeds in an area nearly equal in extent to that of *fasciata*, has not produced local varieties; the non-migratory *Megascops asio* shows great geographical variation, while the migratory *Asio accipitrinus*, though almost cosmopolitan in its breeding area, shows no tendency toward such variation. And, in fact, an examination and comparison of List III with Lists I and II, will lead to the conclusion, that given any two species of equally extensive breeding areas, the one with the smaller range of periodic migration will, as a rule, evince a greater tendency to produce geographical varieties than will the species with the greater range of migration. This conclusion may be concisely formulated as follows; *it is the rule that the amount of geographical variation in species with more or less extensive breeding areas, stands in inverse ratio to the extent of its periodic migrations.* Naturally, this law is only applicable to species with extended breeding areas, since diverse conditions in different sections of this area are necessary, according to the theory of Natural Selection, for the production of geographical subspecies or varieties; and in a limited breeding area, throughout which the conditions of the environment are similar, there could be no cause to produce geographical varieties, irrespective of the migratory or non-migratory habits of the species.

I have not meant to imply, in the preceding pages, that species with migration ranges of 30° lat., or more, are all sharply definable, *i. e.*, that such species are never divisible into geographical varieties; but, on the contrary, that this tendency to produce geographical races is less in the species with extensive migrations, than in those with shorter ranges of migration. For it is usual, even in species with extensive migrations, whose

breeding areas are extraordinarily great, so as to include the whole of the arctic region, or northern America together with northern Eurasia, for them to subdivide into two geographical varieties, occupying respectively the eastern and western hemispheres. Thus, the eurasiatic *Colymbus nigricollis* is represented by a variety (*californicus*) in western North America; and to give other examples where an eurasiatic form, which undertakes long periodic migrations, is represented by a geographical variety in North America, may be mentioned one species of *Fratercula*, 1 *Uria*, 1 *Larus*, 1 *Hydrochelidon*, 2 *Aythya*, 1 *Glaucionetta*, 1 *Somateria*, 1 *Anser*, 1 *Tringa*, 1 *Limosa*, 1 *Charadrius*, 2 *Falco*, 1 *Pandion*, and others. But no species with extensive migration ranges shows any tendency to geographical variation, unless its breeding areas are also very large in extent. And the species with the least demonstrable tendency to produce local races, are those in which the wing power is greater, and the range of migration more extensive, than in any other species of birds, namely, those enumerated in List I. Further, we find it to be the rule, that in those avian families most of the species of which undertake long migrations, if species are present which are divisible into geographical varieties, that these latter are more restricted in their migrations than the former; examples are *Uria troile*, *Rissa tridactyla*, *Fulmarus glacialis* (only North American species of the family presenting geographical varieties), *Rallus longirostris*, *Porzana jamaicensis*, *Aegialitis wilsonia* and *Ae. meloda*, and others. After the consideration of these facts it is certainly permissible to conclude that, as a rule, species which undertake annual migrations of comparatively great extent, through distances of 30° lat., or more, evince no tendency to give rise to geographical varieties, unless their breeding areas are very extensive; and, conversely, that species which do not undertake extensive migrations, owing to insufficient wing power or to some other cause, and which occupy broad breeding areas, have the tendency to produce geographical varieties. Consequently, also, extended migration acts as a check upon the production of varieties; and the extent of the range of migration will, therefore, stand in inverse ratio to the amount of geographical variation

evinced. Thus the postulate of Darwin, that wide-ranging species vary most, must be modified after a consideration of the facts given here. But to pass over to certain apparent exceptions to the rule. *Falco columbarius*, breeding chiefly north of the United States, and migrating in winter as far as South America, has a variety (*suckleyi*) on the Pacific coast from Sitka to California; *Helminthophila ruficapilla*, breeding as far north as Hudson's Bay, and migrating in winter as far as Guatemala, has a variety (*gutturialis*) from the Rocky Mts. to the Pacific coast, in winter to Mexico; and a number of similar cases could be mentioned, where the species, although it has a wide range of migration, and a breeding area which is not extraordinarily extensive, has, nevertheless, the tendency to geographical variation. But such apparent exceptions to the rule are, in fact, not valid objections, since in these cases the geographical variety is much more restricted in the range of its migration than the type species, or *vice versa*. And in any of these cases, the species, including the variety, is to be regarded as a number of individuals, some of which undertake extensive migrations, while others migrate not at all or through much shorter distances. Therefore, these are not true exceptions to the law, that the extent of the migration stands in inverse ratio to the amount of the tendency to produce geographical varieties; since a number of the individuals do not undertake extensive migrations. Real exceptions may, however, be found in such cases where the individuals of the type species as well as its varieties make prolonged periodic migrations; and after a careful examination of all the North American species and their varieties, I have found only four species which represent such exceptions to the rule: *Dendroica æstiva*, with its variety *morcomii*, *Seiurus noveboracensis*, with the subspecies *notabilis*, *Sylvania pusilla*, with the variety *pileolata*, and *Turdus ustulatus*, with its eastern variety *swainsonii*. These four species represent cases where, with not very extensive breeding area, both races of the species possess extensive migration ranges. But I think that the importance of these cases as exceptions to the rule is diminished, when we consider that in each case the migration route of the variety is different from

that of the species, one being west of, while the other is east of the Rocky Mts. And hence, since not only in its breeding area but also in its migration range, the variety is subjected to conditions of environment different from those influencing the type species, we would naturally expect that the species (as a whole) would become differentiated into two geographical races.

The reason for the law, that extensive migration acts as a check upon the production of geographical varieties, is not far to seek. The barn swallow, for instance, remains in its breeding area from four to five months each year, spending the remainder of its time, except that consumed by its actual migration to and fro, in its tropical winter quarters. Roughly speaking, we may say that it spends about half a year in its breeding area, and the remainder in its winter home. In other words, the swallow is subjected to one environment for half the time of its existence, and to a more or less different environment during the remainder of its life. The result of this on the organism is obvious: the action of the two environments during approximately the same length of time, would prevent it from becoming more particularly adapted to the one than to the other, and would lead to the production of more generalized characters, fitted to respond more or less equally to both environments. In this way individuals of the species could not become especially adapted to a certain portion of the breeding area, if such adaptations should be unfavorable for its existence in the winter quarters, and *vice versa*; in other words, the influence of the winter environment acts as a check upon the acquisition of adaptations suited alone to the summer environment. This is, to my mind, the only adequate explanation for the law that extensive migration exerts a check upon the production of geographical varieties. Species with wide-ranging breeding areas, on the other hand, but with none or only restricted migrations, may give rise to geographical varieties, suited respectively to the diverse conditions found in different portions of its habitat, since such species are influenced by the conditions of but one environment, owing to the absence or restriction of migration.

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